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ON THE ORIGIN OF DOUBLE-YOLKED EGGS.

OTTO GLASER.

INTRODUCTION.

By comparing five cases of double eggs that happened to fall into his hands, with a considerable number described in the literature, Parker ('06) was able to divide these abnormalities, on the basis of the factors probably involved in their production, into three classes: "First, those whose yolks have come from an abnormal ovary, but have passed through a normal oviduct; secondly, those whose yolks have come from a normal ovary, but have passed through an abnormal oviduct; and finally those produced by an ovary and oviduct, both of which have been abnormal in their action" (p. 17).

To the first group belong eggs which contain ordinarily two yolks, surrounded either by individual vitelline membranes or by a common one. The second class is made up of eggs in which normal yolks are imbedded in abnormal secondary envelopes, whereas the third is composed of cases in which one egg, consisting usually of shell, shell-membranes, albumen and a small yolk, is enclosed in an outer one of normal construction. Nine cases found in the literature by Parker, four additional ones studied by himself, as well as some of those referred to by Hargitt in a neglected paper ('99) and in a later one ('12), belong to this group.

In this article I shall report observations on a case belonging to the first class, and I do this, not because double-yolked eggs are sufficiently rare to warrant further description, but because I have been unable to find in the literature accessible to me any account of the ovarian abnormalities associated with the production of this type of egg. In fact from Parker (*loc. cit.*, p. 16) one gains the impression that these peculiarities are hardly marked enough to justify the use of the word "abnormal." Thus he says: "The laying of eggs with two yolks may become, as Landois ('78, p. 24) declares, almost habitual with certain

hens. Bartels ('95, p. 143) states that the hen that laid the double egg described by him had often laid such eggs, and Immermann ('99, p. 8) records the case of a hen that laid such an egg about every eight days. Apparently this is as much an organic peculiarity of certain hens as is the production of twins by certain individuals in the human species, and while it may be called abnormal in that it is unusual, it is in no sense indicative of serious organic derangement or disease."

Despite the fact that the origin of double-yolked eggs can be attributed, as it is by Parker, to an ovarian peculiarity, such as the simultaneous discharge of two yolks from separate follicles, or the rupture of one follicle containing two yolks, there nevertheless are two other possibilities. In the first place, an ovum discharged into the infundibulum might fail to be moved downward by peristalsis until the ovary had discharged a second time, in which case we might be dealing either with a deficiency of substances normally inducing these movements, or with subnormal irritability on the part of the oviduct. In the second place, the "organic peculiarity of certain hens" may have an ovarian basis decidedly "indicative of serious organic derangement" if not of disease. The ovary which I have studied is certainly pathological although I cannot conclude that the conditions found are the only ones that induce double-yolked eggs, or that they always do so.

Unfortunately the bird on which my data are based died during my absence and the oviduct was not preserved. However the ovary seems to me capable of explaining why she laid abnormal eggs, although this does not show that the oviduct was normal either in structure or in action. Normality however seems likely, for if there had been peristaltic difficulties it seems reasonable to suppose that occasionally at least an egg abnormal in other respects would have been produced. This is not known to have happened in the five years during which this hen was under fairly constant supervision.

CLINICAL HISTORY OF THE INDIVIDUAL.

The bird in question, a white leghorn belonging to Mrs. Wm. Looker, of Ann Arbor, was hatched in the spring of 1906 and lived

until June, 1911. She was a beautiful example of the breed, but had an unusually large comb. She was a loud and boisterous cackler, and always made a great fuss after laying. Apparently she never exhibited any tendency to set. Although it cannot be stated with certainty that she never laid normal eggs, it is certain that a very large percentage was abnormal.

The eggs during her last year measured on an average 7.5 cm. in their long diameter, 4.5 cm. in their short. The yolks, always in individual vitelline membranes, were equal in size with an average diameter of 3 cm. They were always in contact, or practically so, and were surrounded by a common jelly mass.

The records are too meager to show whether there was any rhythm in her laying. On occasion she laid double-yolked eggs on two or even three successive days. Spells of hyperactivity such as these were frequently followed by periods of indolence lasting from one to several weeks. Sometimes she would lay every other day for a period.

Although the eggs were always large they decreased in later years. Even then laying caused difficulties as evidenced by noises suggestive of struggle. After a period of laying the bird nearly always "moped," hanging her head and refusing to eat. These sick spells were not noticed during the first year or two, although there was never any eagerness for food.

I have given these details because they may be valuable as clinical symptoms, and because they show that the ovary, which, as we shall see, was abnormal structurally, was so physiologically as well. In fact I am inclined to think that the structural peculiarities of this organ are a consequence primarily of some physiological defect, and that the abnormal spatial relations brought about in this way gave the physical basis for the production of double-yolked eggs.

THE ANATOMY OF THE OVARY.

The ovary was removed immediately after the death of the bird and fixed in Zenker's fluid by my brother, R. W. Glaser. The gross appearance as well as numerous details are reproduced in Fig. 1, which I made by first printing an outline of the organ through glass on blue-print paper, and after transferring this to bristle board, filling in the necessary minutiae freehand.

Even a casual glance shows that this organ is markedly abnormal. Most striking of all is the presence of many medium-sized follicles which, instead of being held to the main mass of the ovary by relatively short, stout necks of tissue, are attached

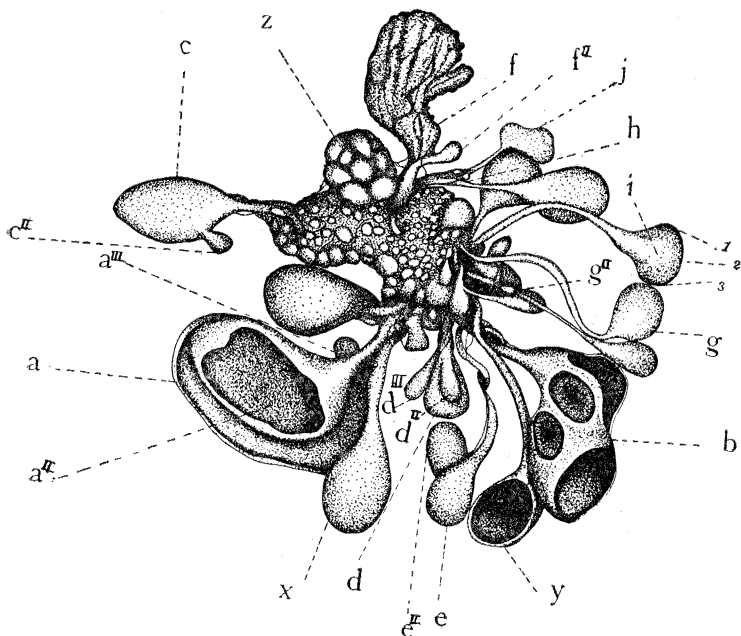


FIG. 1. Abnormal ovary of hen that laid double-yolked eggs. Description in text, p. 178.

by suspensoria more or less twisted and at times over 3.5 cm. in length. Originally these appendages formed a complicated snarl. To facilitate both drawing and description they were carefully dissected apart as in the figure.

Four other features, some of them equally striking, are worthy of note. First are the compound follicles, *a* and *b*; second, apparently budding follicles at *c*, *d*, and *e*; third, apparently branching suspensoria, *f*, *g*, and *h*; and finally a considerable number of fine threads running at various angles from one suspensorium, follicle, or portion of the central mass, to another.

The origin of these various structures can be inferred with reasonable certainty in most cases. As far as the nature of the suspensoria is concerned, I think there can be little doubt,

although there are at least two possibilities as to the mechanism of their development. Sections show that they are composed entirely of connective tissue, and that they may or may not possess a lumen. Blood vessels are abundant. From these facts, as well as from the total absence of granulosa cells, I conclude that the suspensoria are not modified follicles, but greatly elongated projections of the ovarian surface, tunica albuginea, filled with stroma.¹

I am not certain how these elongations have arisen. It is conceivable that they are the products of abnormal growth; it is equally conceivable that they are the result of stretching, due to weakness or readiness to flow on the part of the tunica albuginea. In a bird in its normal upright position, the sudden development (Riddle, '11) of a large yolk mass in a given follicle must seriously increase the load sustained by the tunica, and if this for any reason is weak, stretching in these regions might easily result. It is interesting in this connection that all of the follicles with long suspensoria are either well along in their growth periods, or are attached to those that are. Comparative study of the compound follicles, of the branching suspensoria, and of the threads makes me incline definitely toward the second hypothesis.

Such study not only suggests that all the structures mentioned are the outcome of one and the same process, but also how the more complicated follicles may have originated. *B* is a good one to begin with. Before dissection the surface of this irregular follicle gave but faint indication of the four completely separate cavities which it contains. Sections of the interfollicular walls show one continuous connective tissue mass bridging the distance from one granulosa to the other. This latter membrane in all the follicles sectioned appears much hypertrophied. It is at least four times thicker than normal and contains quite large intercellular spaces or lacunæ.

How such a complex follicle could have originated can be

¹ This naturally suggests the question whether the enlargements at their distal ends are really follicles, or merely abnormal structures superficially resembling them. The discovery of large yolks with smooth surfaces within these bodies, as well as the presence of fibrosæ and granulosa all in proper relation, leaves no doubt that we are dealing with genuine egg follicles.

answered by studying the others. Follicle *c* suggests that compound follicles might have originated by a process of budding. To test this view part of the wall of *c* together with the attached follicle *c''* was cut into sections 10μ thick. To my surprise no connection whatever between the lumina of the two follicles could be found. The place where this was expected showed the granulosa and fibrosa of both, and between the fibrosæ, a thick connective tissue mass highly vascularized. I examined other apparently branching follicles, such as *e*, and again found the same thing true. In certain other instances connections between adjacent follicles do exist, but these are not via the necks of the attached follicles, but through their sides, and must therefore have come about secondarily by the disappearance in these places not only of the inter-follicular tissue, but also of the granulosa and fibrosa. If *c''* then is not a bud, how did it come to occupy its present position?

In *d*, follicles *d''* and *d'''* are attached to the main suspensorium by short necks of their own. These however are so completely fused proximally with the suspensorium of *d* that their independence is largely obliterated. *E''*, although firmly fused to *e*, really has a suspensorium of its own, but this is reduced to an extremely fine thread, visible as an independent attachment only in one or two places. *C''* upon careful examination proves also to have indications of an independent attachment to the central ovarian mass. The threads therefore are reduced suspensoria, and the compound follicles are fusion products.

The question how these fusions occur remains to be answered. Indications as to how these could have come about are contained in the facts just discussed, for these suggest that one follicle is carried away from the central ovarian mass by another. If this is true, we should be able to discover various stages in the process. Accordingly we can interpret *b* as a late stage in which intimate union has occurred among the follicles distally, whereas proximally the suspensorium of the group shows the multiple nature of its origin by its distinct division into a number of strands. *A* is another late stage, only here the follicles seen are larger than in *b*, their fusion is less complete, and *a''* has worked its way into *a* so that the yolk of the latter came to lie between

the granulosa of the outer follicle and the connective tissue covering of the inner one. In this case, too, dissection clearly exposes the compound nature of the suspensorium. *C*, *d*, and *e* represent stages of fusion less complete than the preceding.

If the suggestions made by these follicles and suspensoria are really correct it ought to be possible to find small follicles not only in places where they are not obvious, but also at various levels of the suspensoria, and this has actually been done. For instance, *a*, prior to dissection, was not obviously double. *J* is

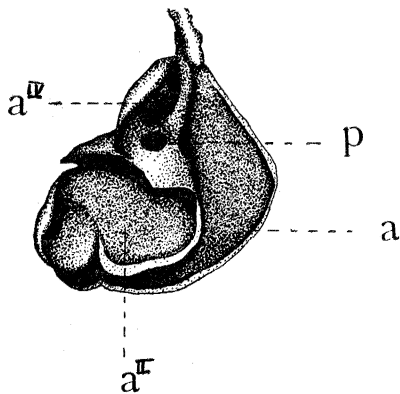


FIG. 2. Dissection of compound follicle, *a*, *a''*, and *a'''*, Fig. 1. Natural size. In this figure *a'''* is omitted. The suspensorium of *a''* has been opened and an additional follicle *a''''* is exposed. The pore, *p*, establishes a communication between the follicular cavity of *a''* and *a''''*.

not simple and somewhat distorted, but double, one follicle being considerably larger than the other; *i* is triple, having a central follicle, 2, and two equal-sized smaller ones, 1 and 3. The one on the right, 3, communicates with 2 by means of a small irregular aperture. No opening connects 1 and 2. In both *i* and *j* the suspensoria appear to be united, and there seems no way of explaining how the extra follicles got into their present position, than by assuming that the same process brought them there that carried the main follicle away from the ovary.

Most illuminating in this connection is the presence of accessory follicles on the suspensoria. Sometimes these are large enough to be easily seen, as in the case of *a'''*, of *f''*, attached to the neck of *f*, a large empty double follicle, and of *g''*; occasionally

they are quite small, like those on the necks of *c* and *j*, whereas at times they may be completely hidden, as in the neck of *a''*, where another follicle was discovered only after the dissection shown in Fig. 2 had been made.

Given weakness on the part of the tunica albuginea, three minor variations of one and the same process are capable of accounting for these different types of follicles. I have tried to represent this in a series of diagrams (Fig. 3).

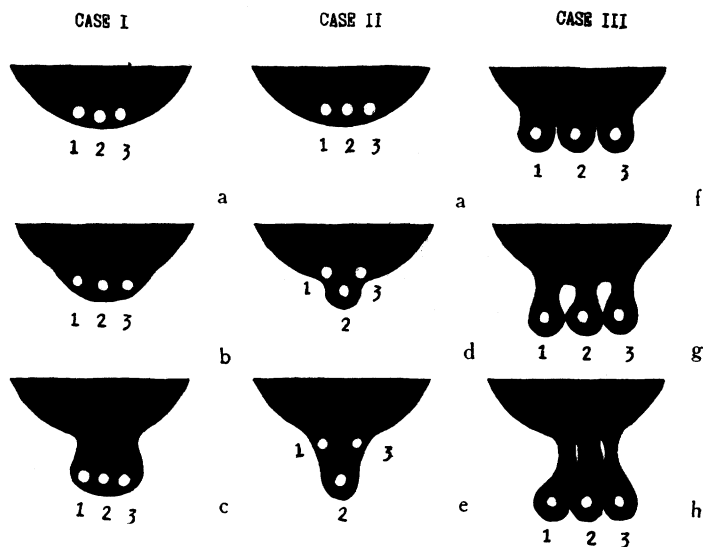


FIG. 3. Diagrams to illustrate the origin of compound follicles. Description in text, p. 182-183.

If we imagine that the ovarian surface evaginates rather broadly beneath egg 2, Case I., diagram *a*, then eggs 1 and 3, which are supposed to lie very close to 2, will be carried away from the ovary, as in *b* and *c*. This would lead to the formation of a follicle of the type *i* and *j*, Fig. 1.

If on the other hand only a very small evagination should take place under egg 2, Case II., its neighbors, 1 and 3, if carried away from the ovary, would not come to lie in such close proximity to 1 in the evagination. In fact they would lie higher up in the suspensorium, *d*, *e*, Fig. 3, and in this manner sufficiently great differences in early distribution would account for the later

development of follicles at various points on the suspensoria as in *a*, *c*, *f*, *j*, etc., Fig. 1.

If, owing to greater distances between the eggs, or to greater stiffness on the part of the tunica, separate evaginations should occur beneath three follicles as in Case III., diagram *f*, Fig. 3, these if not too remote from one another might give rise to a triple follicle, having a common suspensorium except near the ovary where its multiple origin would still be apparent upon close examination. These processes, represented diagrammatically in *g* and *h*, would give rise to complexes similar to *a* and *b*, Fig. 1. If the number of follicles involved were greater, more complicated results would follow. The possibilities of greater complication are clearly indicated by a group of relatively young follicles such as *z*, Fig. 1, as well as by instances in which follicles, of patently distinct origin proximally, have fused distally with others with whom they were brought into contact secondarily by mere accident. Good examples of adhesions of this kind are follicles *x* and *y*, Fig. 1.

In its relation to the production of double-yolked eggs, this ovary is full of suggestions. Follicle *f*, Fig. 1, is an empty double one, and there can be little doubt that it was instrumental in the production of one of the abnormal eggs. Follicles *a* and *a''* contained yolks of essentially the same size, and there seems to be no good reason for doubting that these two would have been shed at the same time. In *b*, the follicles fall into two groups of two each. In one of these they are distinctly larger than in the other, but the follicles within each group are of the same size. It seems likely that in this complex we have the physical basis for the production of two double-yolked eggs in rapid succession. *Z* suggests the possibility of a series of abnormal eggs such as this bird is known to have laid on several occasions.

PHYSIOLOGY OF THE OVARY.

The morphological findings and their interpretation leave open the question as to how one may picture the physiology of this organ. Follicle *b*, Fig. 1, demonstrates the possibility of relatively independent growth on the part of two groups of eggs, as well as the possibility of synchronism in eggs belonging to the

same group. How this can be is answerable by assuming that the vascular supply to the two groups was different, whereas to the individual members of each group it was practically the same. The physical basis for this might easily be found in the character of the fusion undergone by the individual suspensoria, for if this should be such as to partially occlude the flow of blood in certain directions, the follicles supplied by the vessels involved would lag behind those furnished with a better supply. That the blood supply to certain follicles must be affected, is clearly shown by the suspensoria which are reduced to mere threads.

In certain instances, however, a follicle despite its reduced suspensorium is practically as large as the neighbor to which it is attached, as in the case of e'' . This suggests the establishment of a secondary blood supply derived from the better equipped follicle. The highly vascular condition of the connective tissue between the granulosa certainly is favorable to this interpretation. In fact in view of the structural relations it is difficult to see how the blood supply could be otherwise than identical in this case.

Identity of vascularization makes another fact understandable. A follicle such as c'' would under normal conditions have a blood supply much less than that of its "host" c . As it probably is dependent on that of c , however, owing to its intimate fusion with it, and the reduction to almost nothing of its own suspensorium, it is likely to have more material brought to it than it can metabolize in normal fashion. This follicle, as well as others of its size similarly placed, showed considerable depositions of yolk in the lacunæ of their hypertrophied granulosa.

This fact is not only suggestive as to the rôle played by the granulosa during oögenesis, but also of the part of the egg itself in initiating the deposition of yolk, for if the ovum in this instance is not supposed to have been less permeable to the raw materials of yolk than the one in the larger follicle, where only traces of yolk could be found in the granulosa, it is difficult to see why the two eggs should have been unequal in size. There must be a period in the ovarian life of an egg when its permeability to certain substances is suddenly greatly increased. Riddle's work ('11) suggests the same thought, but this abnormal ovary

indicates that the conditions followed by increased permeability are to be looked for in the egg. If ova in the same state have an identical blood supply they will undergo equivalent growth, but mere identity in their circulation does not insure this.

Although these considerations are necessarily speculative, their possible relation to more remote matters may be briefly mentioned. It is certainly a remarkable fact that in the human ovary, to mention a case among mammals, and in the hen's ovary, to mention one among birds, normally one egg ripens after another, whereas in the ovaries of amphibians and fishes thousands of eggs may ripen at one time. It is quite possible that the conditions which in the one case lead to an abnormality are identical with those which in the other give a typical result. In no case do all the eggs contained in any of these ovaries ripen at the same time. This certainly points to alterations in the permeability of the ovum as a factor in the initiation of its growth period, and suggests that these changes are directly traceable to the activity of the egg. The fusion of normally distinct follicles in the hen's ovary brings about secondarily an identical vascularization and thus accidentally duplicates the nutritive conditions prevalent in the ovaries of certain other forms.

Identity of blood supply then is suggested as an explanation of the synchronic yolk formation in these eggs, whereas a change in permeability undergone independently on the part of the eggs themselves introduces this period of growth. This change in permeability must necessarily also be synchronic if double-yolked eggs are to be produced, but how this synchronism is brought about in certain eggs, and how it is prevented in others, cannot be profitably discussed in our present state of knowledge.

The important thing after all is that a bird's ovary, with follicles secondarily fused as described in the preceding pages, does actually give rise to a series of double-yolked eggs, and this remains true even if my suggestions as to the development and physiology of this organ should prove to be entirely wrong. It is to be hoped that the clinical symptoms given may aid in the discovery of further material upon which more detailed studies in the living state could be carried out with great advantage to

our knowledge of the more obscure points in the physiology of egg-production.

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